E.D. R
E&A

Vol. 108. Part 2. Pp. 21–36. 3 figs. 10th April, 1956.

COMMONWEALTH INST. OF ENTOMOLOGY LIBRARY
11 APR 1956
GENERAL Eu. 344
SEPARATE

THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

	PAGE
MATTINGLY, P. F., B.Sc., F.R.E.S. Species Hybrids in Mosquitoes	21–36, 3 figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W. 7

Price 6s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded 1833. Incorporated by Royal Charter 1885.

Patron:

HER MAJESTY THE QUEEN.

OFFICERS AND COUNCIL FOR THE SESSION, 1956–1957.

DR. W. J. HALL, C.M.G., M.C. *President.*

MR. P. FREEMAN
DR. H. E. HINTON
MR. W. H. POTTS
} *Vice-Presidents.*

DR. N. E. HICKIN, *Treasurer.*
MR. E. B. BRITTON, *Secretary.*
MR. J. BALFOUR-BROWNE, *Editor.*

Other Members of Council.

MR. R. F. BRETHERTON, C.B.
MR. W. V. HARRIS.
MR. T. G. HOWARTH.
DR. H. B. N. HYNES.
MISS D. J. JACKSON.
MR. R. W. LLOYD.
DR. K. MELLANBY, C.B.E.
MR. H. L. G. STROYAN.
MR. F. T. VALLINS.
MR. H. B. WILLIAMS, Q.C.

MISS E. EVANS, *Registrar.*

Finance and House Committee.

DR. K. MELLANBY, C.B.E. (Chairman).

DR. J. R. BUSVINE.
MR. W. V. HARRIS.
DR. W. F. JEPSON, O.B.E.
MR. A. T. THOMPSON.
DR. I. H. H. YARROW.

Publication and Library Committee.

MR. PAUL FREEMAN (Chairman).

MR. R. F. BRETHERTON, C.B.
DR J. L. CLOUDSLEY-THOMPSON.
MR. E. O. PEARSON.
MR. W. H. POTTS.
MR. H. L. G. STROYAN.

Committee for the Protection of British Insects.

MR. H. M. EDELSTEN, O.B.E. (Chairman).

MR. R. B. BENSON.
MR. R. F. BRETHERTON, C.B.
LIEUT.-COL. C. A. W. DUFFIELD, M.C., J.P.
DR. B. M. HOBBY (*and representing the Society for British Entomology*).
CAPT. R. A. JACKSON, C.B.E., R.N.
LIEUT.-COL. W. B. L. MANLEY.
DR. A. M. MASSEE, O.B.E.
MR. A. ROEBUCK, O.B.E., N.D.A.
MR. N. D. RILEY, C.B.E. (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society
   Prof. G. C. Varley, appointed 1952.
   Mr. N. D. Riley, C.B.E., appointed 1955.
2. **Local Committee of Management of Wicken Fen.**
   Mr. H. M. Edelsten, O.B.E. (nominated by Committee for the Protection of British Insects).
3. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. N. D. Riley, C.B.E., appointed 1955.
4. **New Forest Association.**
   Mr. C. W. Mackworth-Praed, appointed 1948.
5. **New Forest Joint Committee.**
   Lt.-Col. F. C. Fraser, appointed 1949.
6. **Council for the Promotion of Field Studies.**
   Dr. W. H. Thorpe, F.R.S., appointed 1944.
7. **Joint Bioclimatic Committee.**
   Dr. B. P. Uvarov, C.M.G., F.R.S., appointed 1945.
   Dr. C. B. Williams, F.R.S., appointed 1945.
8. **Yorkshire Naturalists' Trust, Ltd.**
   Dr. W. D. Hincks, appointed 1946.
9. **The Biological Council.**
   Dr. N. E. Hickin, appointed 1952.
10. **The Parliamentary and Scientific Committee.**
    Dr. N. E. Hickin, appointed 1953.
11. **British Co-ordinating Committee for Nature Conservation.**
    Mr. E. B. Britton, appointed 1954.

SPECIES HYBRIDS IN MOSQUITOES.

By P. F. Mattingly, B.Sc., F.R.E.S.

(*British Museum (Natural History)*.)

Manuscript received April, 1955.

(Read 2nd November, 1955.)

With 3 Text-figures

The present paper does not purport to review the whole of the literature relating to species crosses in mosquitoes. This has recently been done very adequately by Kitzmiller (1953*a*).[1] Instead it is proposed to single out for special attention certain observations and experiments either because it is considered that these have been wrongly interpreted (as in the case of crosses between *Aëdes aegypti* Linnaeus and *Aëdes albopictus* Skuse) or because they appear to merit more extensive discussion owing to their wide biological interest. The principal aim of the paper is to interest the geneticist in the various groups of mosquitoes discussed which are of great medical importance and involve species excellently suited to laboratory culture. At the same time it is hoped that the taxonomist and the epidemiologist may be reminded of the potential usefulness of a genetical approach to their work. For the furtherance of these ends notes have been included, wherever these seemed appropriate, on the taxonomy, bionomics, distribution, population genetics and phenotypic variability of the species under consideration. The substance of this paper was communicated in part to the Royal Entomological Society of London at its meeting in November, 1953, and in part to Section D of the British Association for the Advancement of Science at its Oxford meeting in 1954. It has not, however, previously appeared in print.

The first crosses here considered are not, strictly speaking, species crosses since they take place between populations of a single species, *Culex molestus* Forskål (*Culex autogenicus* Roubaud of some authors), or, as some workers, including the present author, would prefer to call it, *Culex pipiens* Linnaeus var. *molestus* Forsk. (see Mattingly *et al.*, 1951, 1953). They have been chosen for consideration because the populations concerned exhibit varying degrees of reproductive isolation and in this respect behave like true species. In general the existence of a high degree of reproductive incompatibility is regarded as the hall mark of a good species, but in the present case special factors must be taken into consideration. The taxonomic problem which arises is discussed more fully below. All that is intended for the moment is to stress the desirability, when employing genetical data for taxonomic purposes, of investigating the cytological background as fully as possible.

[1] Kitzmiller's review can be brought up to date by reference to Barr (1954), Callot (1954), Dobrotworsky and Drummond (1953), Kitsmiller (1953*b*), Laven and Kitzmiller (1954), Rozeboom (1953, 1954), Rozeboom and Gilford (1954*a*, *b*), Woodhill (1954), Dobrotworsky (1955) and Laven (1955 and 1956).

The first crosses between geographically representative strains of *Culex molestus* were made by Marshall and Staley (1937) and Marshall (1938), using strains from London, Paris, Hull and the Portsmouth area in all possible combinations. Even within this limited material all three theoretically possible results were encountered. Thus the Hull-Paris cross was successful in both directions, the Hull-London cross in neither and the crosses between the Portsmouth strain and the others were successful only when using Portsmouth males and not when using Portsmouth females. More recently this work has been repeated, using many more strains, Ghelelovitch (1952), Laven (1951, 1953 and in Mattingly *et al.*, 1951, 1953) and Laven and Kitzmiller (1954). The latter authors and Simonetti (1952) also employed strains of other members of the *Culex pipiens* complex (*C. pipiens* and *C. pipiens* ssp. *fatigans* Wiedemann (usually referred to by American authors as *C. quinquefasciatus* Say)), but for present purposes it is necessary to consider only var. *molestus* and only Laven's work on this form. This work has been mainly devoted to two aspects of the problem, firstly the geographical distribution of the various mating types and secondly the cytological basis of the reproductive incompatibility which these mating types exhibit. Under the first heading it has been shown that "there exist at least eight different groups of *molestus* populations, some of which are genetically isolated and some correlated by a strictly unilateral flow of genes". The distributional mapping of these populations will involve very much time and labour, but until it is completed any attempt at formal taxonomic treatment will clearly be premature.

Laven's cytogenetical work (like that of Ghelelovitch which followed similar lines and produced identical results) was based on techniques employed by L'Héritier and his collaborators in studies on carbon dioxide sensitivity in *Drosophila* (see below). His results can best be illustrated by reference to two of his strains, a North German one from Hamburg and a South German one from Oggleshausen in Upper Swabia. Taken together these provide an excellent example of non-reciprocal or unidirectional compatibility. Thus, whereas males of the Oggleshausen strain produce just as many viable offspring when mated with Hamburg females as they do with females of their own strain, almost no viable offspring are produced when Hamburg males are mated with Oggleshausen females (fig. 1, *a*). The actual number of fully viable offspring from the latter cross is not more than one per five hundred eggs, usually very much less.

By backcrossing offspring of both crosses to the parent strains Laven was able to demonstrate the occurrence of a purely maternal type of inheritance. In whichever way the backcross was made the offspring were found to behave precisely like the original maternal strain. Thus male offspring from a Hamburg mother behaved like Hamburg males and were unable to produce viable offspring with Oggleshausen females as their Oggleshausen fathers had done, while male offspring of an Oggleshausen mother were able, unlike their fathers, to produce viable offspring with females of either strain just as would Oggleshausen males.

In formulating a hypothesis to account for these phenomena Laven ruled out the possibility that the maternal inheritance was parthenogenetic in nature. For this purpose he used marker genes to show that a fusion of nuclei occurs. At the same time he showed that the lethal factor concerned operates, in the

main, only when the later embryonal stages are reached within the egg. Finally he showed that the factor was transmitted to the offspring in the cytoplasm and was independent of the type of nucleus which this cytoplasm contained. This he did by mating hybrid females derived from a Hamburg mother with Oggleshausen males. The female offspring of this cross were again mated with Oggleshausen males and so on through twenty successive generations. At the end of this time it was concluded that the cytoplasm, derived almost entirely from the original Hamburg mother since the contribution from the sperm is negligible in bulk, must contain a virtually pure Oggleshausen nucleus. Backcrosses at every stage failed to show any modifying influence

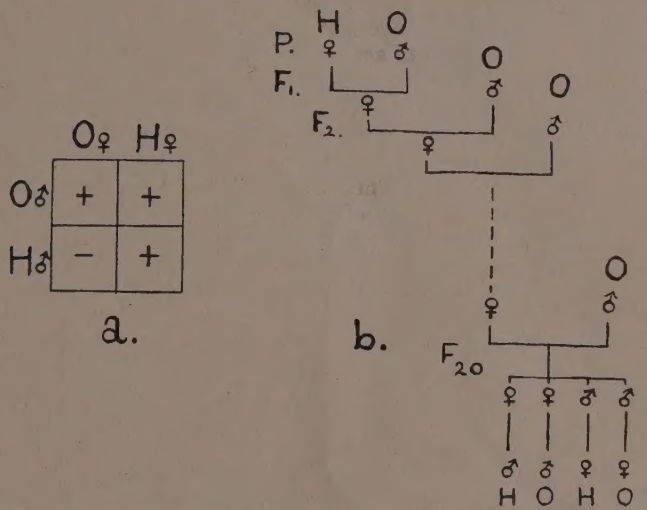

FIG. 1.—Crossing experiments with two German strains of *C. pipiens* var. *molestus*. (*a*) Non-reciprocal compatibility of Hamburg and Oggleshausen strains. (*b*) Demonstration of the cytoplasmic basis of reproductive incompatibility in these strains. H. Hamburg strain. O. Oggleshausen strain. The backcross is shown only for F20 but was, in fact, performed with each generation.

exerted by this nucleus and throughout the experiment the hybrids continued to behave like normal Hamburg males and females with respect to their reproductive compatibility (fig. 1, *b*).

In conclusion Laven pointed out that the back cross of the 20th generation hybrid male to the Oggleshausen female proves that the lethal factor is carried in the cytoplasm of the sperm since the latter contained a normal Oggleshausen nucleus despite its incompatibility with the Oggleshausen ovum. As already noted, similar results have been obtained with the carbon dioxide sensitivity factor in *Drosophila* and similar conclusions have been drawn. In this case, however, the work has proceeded further and it has been shown that the factor can be introduced by injection or implantation into previously unaffected flies and will then find its way into the gonads and be transmitted to the offspring in the cytoplasm of the germ cells. L'Héritier has pointed out that in some respects the factor behaves like a cytoplasmic gene and in others it behaves like

a virus (for a review of this work see, e.g., L'Héritier, 1951). Work on implantation and injection in mosquitoes is as yet only in its early stages and, so far as is known, no conclusive results have as yet been obtained.[2]

Before proceeding to a consideration of maternal inheritance in another group of culicine mosquitoes it is perhaps desirable to summarise certain general features of the *Culex pipiens* complex to which *C. molestus* belongs. Four principal members of this complex are at present recognised. Three of these, *C. pipiens*, *C. fatigans* and *C. molestus*, have already been mentioned. The fourth is *Culex pipiens* var. *pallens* Coquillett, which is widely distributed in China and Japan. It is intermediate in morphological characteristics between *C. pipiens* and *C. fatigans*. It is not clear whether it is a hybrid between these forms or an anectant form from which they themselves have been derived. Its biology has recently been rather fully discussed by Hosoi (1954). *Culex pipiens* is the common domestic mosquito of most of the Palaearctic and Nearctic regions. It also occurs widely in the East African highlands and in South Africa and an isolated population has been reported from Argentina. The form of *C. pipiens* occurring in Australia has recently been described as a distinct subspecies (Dobrotworsky and Drummond, 1953). *C. fatigans* is the counterpart of *C. pipiens* in the tropics and subtropics where it is a very common, widespread, domestic mosquito of great medical importance.[3] Despite this fact its infraspecific taxonomy remains almost wholly unstudied. There are indications that at least three forms occur in the East African lowlands, the central African plateau and West Africa respectively. The position in the last named area is particularly obscure. *Culex pipiens* (or *molestus*) has been recorded from Dahomey by Huttel (1950) and the Paris Museum has a series from Kankan in French Guinea, while the Washington Museum has a set of male terminalia from Accra, Gold Coast. It seems probable that both *C. pipiens* and *C. molestus* have been repeatedly introduced and the latter, at any rate, may have been able to establish itself here and there. If this is so the biological peculiarities of the West African *C. fatigans* may be the outcome of hybridisation. *C. molestus* was first described from Egypt and has recently been studied there in some detail (Knight and Abdel Malek, 1951). It differs from *C. pipiens* in a number of small morphological characters which tend to intergrade in parts of their joint range and which assume an intermediate form in laboratory hybrids (Callot, 1947, 1954; Ghelelovitch 1950). The two are identical with respect to their male terminalia but differ markedly in this respect from *C. fatigans*. In its other morphological characters and in all its outstanding biological characters (anthropophily, homodynamy, stenogamy, underground breeding, DDT-resistance), except one, *C. molestus* resembles *C. fatigans*. The one exception is its possession of the ability to produce viable eggs without a blood meal (autogeny), a character which has greatly interested physiologists (for review see Clements, 1954). In this character it differs from both *C. pipiens* and *C. fatigans*. The autogeny rate in naturally occurring populations is very low in Egypt and very high in Palestine. Outside these areas and certain others in North Africa the natural autogeny rate has not been studied quantitatively and this is a serious handicap to our understanding of the

[2] For further information see Laven 1955, 1956.

[3] It is, however, much more local in its occurrence in some parts of the world than is commonly realised. The same is true of *Aëdes aegypti* (*infra*).

distribution of the complex in Europe. In crossing experiments autogeny is inherited as an almost wholly recessive character, but it tends to build up very rapidly in cage colonies as a result of unconscious selection. In northern Europe the distribution of *C. molestus* appears to be sporadic and largely urban. This is probably due to its inability to hibernate (homodynamy) although Laven (*in* Mattingly *et al.*, 1951) has suggested that it may be maintained through the winter in rural areas by hybridisation with the heterodynamous *C. pipiens*. In southern Europe and the Mediterranean region generally it appears to be much more widely distributed. It also occurs widely in the United States and is thought to have been introduced from there into southern Australia during the last war. In Australia it has hybridised extensively with *C. fatigans* in nature (Drummond *in* Mattingly *et al.*, 1951). In general the various members of the complex hybridise very readily in the laboratory (for references see Kitzmiller, 1953) and Rozeboom and Gilford (1954) have shown that little or no selective preference for mates of their own subspecies is shown by *C. pipiens* and *C. fatigans*. The recorded failures may possibly be explicable on the basis of Laven's discoveries. Farid (1949), Sundararaman (1949), Barr and Kartman (1951), Kartman (1953) and Knight (1953) have studied the hybridisation of these two forms in the United States (and see Rozeboom *in* Mattingly *et al.*, 1951). From the occurrence of wild intermediates it would seem that some hybridisation takes place in nature, though its extent is not yet known. This is understood to have been the subject of a recent investigation, the results of which may soon be ready for publication. The extent of hybridisation in other parts of the range is still unknown. South Africa and the region of the boundary between the Palaearctic and Ethiopian regions in Africa and Arabia seem likely areas, but specimens so far examined have not been of clear-cut hybrid type. The Persian Gulf area is also suspect owing to records of larvae of intermediate type, and intermediate altitudes in the East African Highlands seem worth investigating. It seems possible, on the other hand, that hybridisation in the United States may have been the result initially of the introduction of *C. pallens* or *C. molestus* into areas outside those which they originally occupied. There are some reasons for thinking that *C. pipiens* is a relatively recent introduction into North America (see Howard, Dyar and Knab, 1915). Certainly the first record from that continent is a very recent one (Bergroth, 1889). A number of published figures of terminalia of *C. pipiens* from the U.S.A. are much nearer the hybrid type than those of northern European *C. pipiens* which tend to show very little variation (see, e.g., Carpenter *et al.*, 1946). Finally, in this connection, mention may be made of the remarkable natural and laboratory hybrids reported by Dobrotworsky and Drummond (1953) as occurring between *C. molestus* and *C. globocoxitus* Dobrotworsky in southern Australia. These species, like *A. aegypti* and *A. albopictus*, have very distinct male terminalia (fig. 2). It might be thought that this would inhibit cross-mating, but it is worth noting that in both cases the phallosomes of the two species concerned are closely similar.

The *C. molestus-C. globocoxitus* hybrids have not previously been described or figured.[4] Two wild hybrid males kindly sent me by Dr. Dobrotworsky differ considerably in their terminalia. One has terminalia which are not

[4] Since going to press a description and discussion has been published by Dobrotworsky (1955).

notably distinct from those of *C. molestus*. The other has terminalia intermediate between those of the two species (fig. 2, *c*). It is interesting to note that in each case a certain degree of anisomorphism occurs as between the

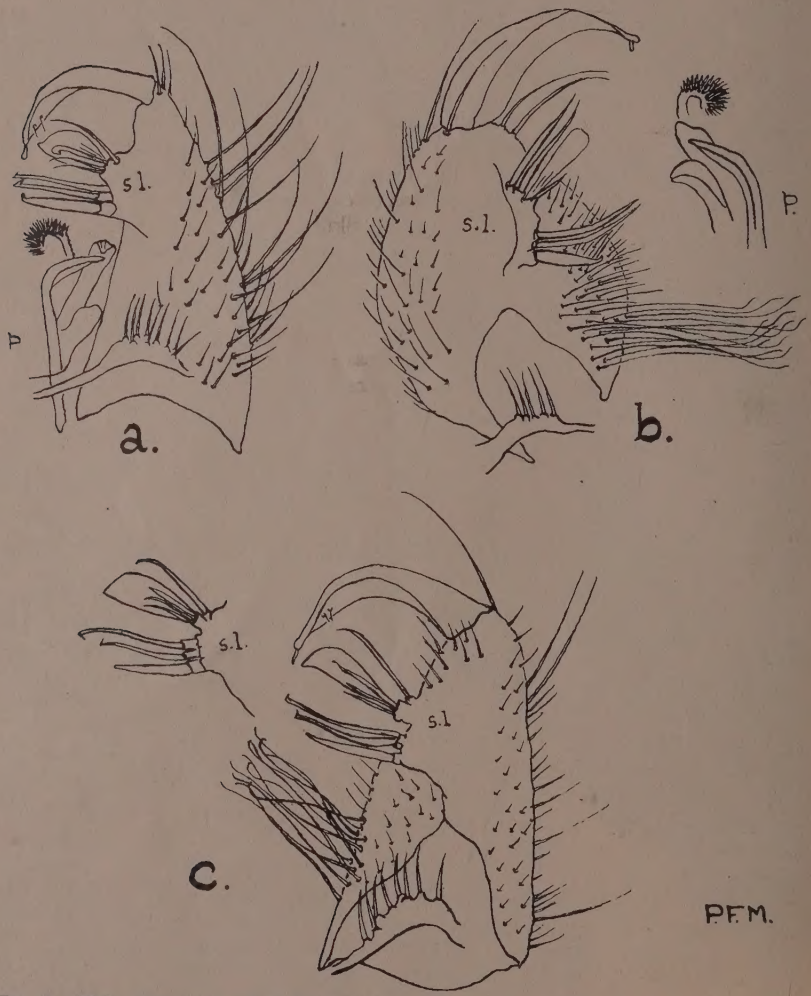

Fig. 2.—Male terminalia of hybridising species. (*a*) *C. molestus*. (*b*) *C. globocoxitus*. (*c*) Wild hybrid showing subapical lobes of the two coxites of the same specimen. *p.*, Phallosome ; *s.l.*, subapical lobe of coxite.

subapical lobes of the two coxites of the same specimen (more pronounced in the specimen figured than in the one resembling *C. molestus*).

A comparative study of a good series of these hybrids and of back-crosses should be most interesting from the point of view of morphogenesis.

Ancillary to these wider studies have been others on serology (employing the mosquitoes as antigens) by Lawlor (1949 and see Rozeboom *in* Mattingly *et al.*, 1951, other work understood to be in progress), on the electrophoretic, paper chromatographic and spectographic analysis of tissue extracts and free amino-acids (references in Micks, 1954), on sex determination (Gilchrist and Haldane, 1947; Qutubuddin 1952), on crossing-over and chiasma formation (Callan and Montalenti, 1947), on somatic mitosis of polyploid nuclei (Schuh, 1951), on chromosome mapping (preliminary note by Kitzmiller and Clark, 1952, further work understood to be in progress) and on the production of X-ray induced mutations (Laven *in press*). Some of these matters will be more fully discussed in the following section dealing with the hybridisation of *Aëdes* (*Stegomyia*) *aegypti* Linnaeus (*Aëdes argenteus* and *Stegomyia fasciata* of early authors) and *Aëdes* (*Stegomyia*) *albopictus* Skuse (*Stegomyia scutellaris* of some early authors, but not in the sense in which that name is here employed).

Waddington (1954) considers that the lethal factor studied by Laven to be, perhaps, the likeliest case on record of a true plasmagene occurring in the higher animals but points to its sporadic local occurrence and "the existence of rather similar factors in certain other nearly related species of mosquito" as raising "the possibility that it may be rather an exogenous virus to which certain local races are adapted." It is not clear to which "other nearly related species of mosquitoes" reference is made. Cytoplasmic inheritance was postulated by Toumanoff (1950) to explain the maternal inheritance of morphological characters in his *A. aegypti-A. albopictus* crosses and Rozeboom and Gilford (1954*b*) again emphasised this possibility in considering Toumanoff's crosses and those made by Perry (1950) between species of the *Aëdes* (*Stegomyia*) *scutellaris* Walker group. Smith-White (1950) put forward a detailed hypothesis on the same lines to account for non-reciprocal compatibility between *Aëdes scutellaris* and a subspecies. Active work on the *Aëdes scutellaris* group is understood to be in progress and final judgement on this group must be suspended although some notes are given below. In the opinion of the present author there are, however, good grounds for rejecting the hypothesis of cytoplasmic inheritance in the *A. aegypti-A. albopictus* crosses and for postulating a chromosomal mechanism to account for the phenomena observed. At this point it may perhaps also be mentioned that the work of Weyer (1936) appears to suggest that maternal inheritance of autogeny takes place in crosses between *C. fatigans* and *C. molestus*, although this is usually regarded as a mendelian character (but see Kitzmiller 1953).

Unlike the members of the *Culex pipiens* complex, *Aëdes aegypti* and *Aëdes albopictus* are morphologically very distinct indeed and are usually placed in two quite different sections of the subgenus *Stegomyia*. They were first crossed by Toumanoff (1937, 1938, 1939, 1950). He was successful in making the cross in both directions, but only very small numbers of viable offspring were obtained when *A. aegypti* was used as the mother. Other workers were successful only in the opposite direction (Downs and Baker 1949; Bonnet, 1950) or were unsuccessful in making the cross in either direction (Simmons, St. John and Reynold, 1930; De Buck, 1942). It is interesting to note that Toumanoff (1939) was unable to cross his Indochinese *A. albopictus* with imported Indian *A. aegypti* in either direction. MacGilchrist (1913) had long before noted that copulations between *A. aegypti* and *A. albopictus* in Calcutta appeared to be

unproductive. This suggests a comparison with the geographical variation in compatibility encountered in *C. molestus*, but the genetics and cytology of the phenomenon were not investigated.

The results of Toumanoff's crosses so surprised him that he had them repeated by an Indochinese assistant (Hoang Tich Try, 1939), who confirmed them in every particular, finding that all the F_1 offspring, as well as those of later generations, appeared as perfectly typical *A. albopictus*, i.e. they followed the mother and showed no observable traces of paternal characters. Downs and Baker and Bonnet, using *A. aegypti* as the mother, likewise found all their

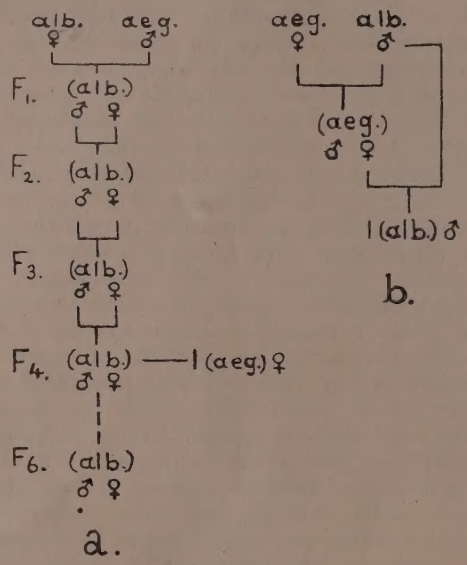

FIG. 3.—Paternal " throwbacks " in crosses between *A. aegypti* and *A. albopictus*, (*a*) by Toumanoff, (*b*) by Bonnet.

hybrid offspring to be apparently typical *A. aegypti*. There appeared to be little or no loss in viability or potency in the hybrid offspring, at any rate in later generations, and Toumanoff was able to inbreed the hybrids for fourteen generations, after which the experiment was abandoned.

Thus far, as we have seen, the resemblance to the *Culex* crosses seems a close one. That there are, in fact, fundamental differences is, however, shown by the fact that in an F_4 generation Toumanoff (1938) obtained a unique female adult which threw back to the paternal species and appeared as a typical *A. aegypti*, though with reduced viability (fig. 3.). This result might be explained by laboratory contamination but this is unlikely since, were it so, more than one "throwback" would have been expected and there would be no reason to anticipate reduced viability. A later experience by Bonnet (discussed below) renders this suggestion, in the author's opinion, quite untenable. This throwback is quite inconsistent with any hypothesis involving cytoplasmic inheritance, since it clearly indicates the survival through four generations of

paternal chromosomal characters. The same applies to the result obtained by Bonnet (1950) when he backcrossed his F_1 hybrids to the paternal *A. albopictus*. The outcome of this backcross was that only one out of 175 eggs hatched and this one produced a typical male *A. albopictus*, again throwing back to the paternal species. These phenomena can clearly not be accounted for by parthenogenesis (as was tentatively suggested by Downs and Baker) or by preconditioning of the cytoplasm by the maternal nucleus (as in the well-known case of inheritance of direction of torsion in the snail shell), nor are they in any way comparable to the phenomena observed in *Culex*.[5] That the whole or a part of the paternal chromosome complement persists in the hybrids while remaining unexpressed in respect to the characters so far studied seems certain. The only comparison which suggests itself is with certain remarkable species hybrids in the plant genus *Oenothera* in which a whole series of self-perpetuating species has arisen as a result of chromosomal translocations coupled with balanced lethal genes (Cleland, 1936, or, for a simple exposition, see Altenburg, 1945).

Further progress in the elucidation of the mechanism involved must depend on direct observation of the chromosomes. It certainly cannot be assumed that the same mechanism is involved in both cases, although it would seem that the superficial appearances are extremely similar. Unfortunately good preparations of the chromosomes of *A. aegypti* are very difficult to obtain. It would seem that the best so far made are those of giant chromosomes from the salivary glands and Malpighian tubules of fourth instar larvae of which photographs are to be found in Sutton (1942). Sutton thought that these might be adequate to show specific differences although the differences which she herself observed were between *A. aegypti* and *C. pipiens* and were therefore intergeneric. There can be little doubt that Sutton's results could be improved if a thorough study were made of the factors involved. Such success as she had appears to have been due to lowering the temperature of the larval environment for several days before her preparations were made. Such a procedure normally leads to the production of unusually large larvae and there can be little doubt that a nutritional factor is involved. This is confirmed by the work of Frizzi (1947) who found that "the conditions (especially nutritional) under which the larvae were reared" were of paramount importance in obtaining his beautiful preparations of salivary gland chromosomes in Anopheline mosquitoes. Recent work on the nutritional requirements of mosquito larvae includes some detailed work on the vitamins of the B group. (Full references can be obtained by working back from Golberg and De Meillon, 1948. For earlier references add Hinman, 1937, and Trager, 1937). Attention is also directed to an interesting note by Joyet-Lavergne (1941) on the uptake of vitamin B_2 in vitro by isolated salivary glands in the related family of the Chironomidae. The relationship of forms with "good" to those with "bad" chromosomes can be remarkably close, as is shown by the fact that *C. fatigans* yields excellent chromosomes while those of *C. molestus* are quite unusable. At an even lower taxonomic level Callan and Montalenti (1947) noted a remarkable difference in

[5] Perhaps worth noting in this connection since it suggests a possible experimental approach is the observation by Kartman (1953) that susceptibility to infection with the parasitic worm *Dirofilaria immitis* is purely maternal in *A. aegypti-A. albopictus* hybrids but not in those between *C. pipiens* and *C. fatigans*.

the physical characteristics of their chromosome squashes as between British and Neapolitan strains of *C. molestus*.

The most obvious indirect approach which suggests itself is the study of the disturbance of the sex ratio in the hybrids. The "normal" sex ratio in *A. aegypti* does not appear to have been adequately studied, but in a series of unpublished studies by the present author 1872 mosquitoes of this species, from about 3000 eggs, gave a ratio of almost exactly 5 males to 3 females. It is interesting to find that almost exactly the same ratio is obtained by combining all the published figures for *A. aegypti-A. albopictus* hybrids. As against this the individual egg batches commonly give ratios well outside the expected range of deviation due to sampling. The nature of the sex determining mechanism in *Stegomyia* is unkown. In *Culex molestus* Gilchrist and Haldane (1947) drew the conclusion that "maleness appears to be due to a single dominant gene". These authors obtained a sex ratio of almost exactly 1 : 1 and the same ratio was obtained for *C. fatigans* in a very detailed investigation by Qutubuddin (1952). No recognisable sex chromosomes have ever been detected in culicine mosquitoes, although Frizzi (1947) claims to have detected X and Y chromosomes in Anophelini.

If it could be shown that successful mating actually takes place in nature between *A. aegypti* and *A. albopictus* this hybridisation would be of considerable practical importance, since both are highly important disease vectors. Rozeboom (*in* Mattingly *et al.*, 1951) considers that mating between these two species does not take place if the males are given a choice between females of their own species and those of the other. It cannot be assumed that such a free choice is always available in nature, but natural hybridisation certainly seems likely to be a rare occurrence. If it does take place then the hybrids would be difficult to detect without backcrossing or the sporadic occurrence of 'throwbacks". Detection would, indeed, be impossible if the statement of all the authors so far quoted that the offspring are identical with the maternal species be accepted. Only Downs and Baker, however, state which characters they examined and it is noteworthy that they omitted one major character, the occurrence of scales on the clypeus, which distinguishes the females of *A. aegypti* from those of almost all other species of *Stegomyia*. It seems possible that, while major characters are inherited from the mother alone, smaller characters may be derived from the father. Something of the sort has already proved to be the case in species hybrids of *Lucilia* (Waterhouse and Paramonov, 1950), studies on which led to the adoption of more refined methods of diagnosis than had previously been employed. In this connection a knowledge of phenotypic variability is clearly essential and this is not at present available for either *A. aegypti* or *A. albopictus*, although an excellent study of the related *Aëdes* (*Stegomyia*) *pseudoscutellaris* Theobald has recently been completed (Marks, 1954). In coastal areas in Africa and in some other parts of the world *A. aegypti* is an extremely variable mosquito (photographs in Summers-Connal, 1926, 1927, whose work clearly showed that this variation is genetical). This is considered to be the result of hybridisation between the local dark forms and pale strains from more arid parts of the range (Mattingly, 1953). These pale strains are commonly known as "*Aëdes aegypti* var. *queenslandensis* Theobald" although it was almost certainly from one of them that Linnaeus (1762) originally described the species. Recent studies by Teesdale (1955)

suggested that differences in behaviour of the two forms might explain certain anomalies observed in the behaviour of *Aëdes aegypti* which were hampering control work in Mombasa. The frequent occurrence of pale coloration in *Culex molestus* and in many "desert" mosquitoes had led the present author to conclude that this coloration might be associated with a cryptozoic habit. With this suggestion in mind Mrs. E. C. C. van Someren very kindly examined a number of *Aëdes aegypti* caught under various circumstances in the Mombasa area and has sent the following figures: In bush, 125 dark (including 19 males), 5 pale (all females); in houses, 7 dark (including 2 males), 232 pale (all females). These figures clearly do not furnish conclusive evidence of the correctness of the original hypothesis, but so far as they go they seem to support it and they certainly suggest that a study of the population genetics of the two forms and their hybrids would produce interesting and useful results.

The only known close relatives of *A. aegypti* are two remarkable pale forms, *A. mascarensis* MacGregor and *A. vinsoni* Mattingly, which are apparently confined to Mauritius (Mattingly, 1953). The Mascarene *A. aegypti* are mainly of the pale form. Mr. J. G. Halcrow suggests (*in litt.*) that they may have been introduced by the Arabs who visited Mauritius about 1000 A.D. In the absence of quarantine precautions their dhows certainly teem with this species. *A. aegypti* has now been eradicated from Mauritius (Halcrow *in* Mattingly and Chwatt, 1954). The fate of the other two forms is not known, but since *A. mascarensis* is a wild form it seems likely that it has survived *A. vinsoni* is known only from one specimen and it seems possible that it may represent the type of aberrant form which tends to appear towards the end of an eradication campaign. It is also possible that both are island forms of "var. *queenslandensis*" of recent origin. Studies of the mating behaviour and hybrid offspring of the three forms and of the type form would be of great interest.

Before leaving the subject of the *Stegomyia* crosses a few words may be said regarding the laboratory bionomics of these species since these are of considerable practical importance for the geneticist. Details of methods for large scale standardised laboratory culture will be found in Christophers (1947). Should these methods be thought too elaborate for small scale experiments it may be pointed out that the production by these and other species of *Stegomyia* of drought-resistant eggs obviates the need for the maintenance of a permanent colony. The eggs can be kept perfectly viable, under appropriate conditions, for at least six months and will then hatch on immersion in slightly polluted water. Adults can be expected in a week or less after hatching and the females will be ready for blood-feeding about 72 hours after emergence. The second generation of eggs will be laid four or five days later and these can be stored as before. A similar technique of periodical hatching and storage was employed by Marks (1954) in her studies on phenotypic variation in *Aëdes pseudoscutellaris*.

The *Aëdes* (*Stegomyia*) *scutellaris* Walker group, contains, as at present constituted, 16 species and 2 subspecies. It is widely distributed from the Maldive Is. in the west (Mattingly, 1954) to Pitcairn I. in the east and Okinawa in the north. It has been exhaustively reviewed by Marks (1954). Five of the included forms have been the subject of hybridisation experiments in the

laboratory. The first experiments were carried out by Woodhill (1950), who crossed *Aëdes scutellaris* and a new subspecies named by him ssp. *katherinensis*. He found that these forms were fully compatible in one direction, normal numbers of viable eggs being produced, and totally incompatible in the other. On back-crossing the male hybrids were found to be wholly incompatible with the females of the paternal strain (*A. katherinensis*). All of the other three possible backcrosses were completely successful. Smith-White (1950) discussed the genetics of these crosses and independently suggested as a working hypothesis an explanation similar to that adduced by Laven in the case of *C. molestus*. Woodhill also crossed the type form and ssp. *katherinensis* with *Aëdes pseudoscutellaris* and found the latter species to be wholly incompatible with either. He considered that, despite the existence of non-reciprocal compatibility, sympatric populations of *A. scutellaris* and *A. katherinensis* (the existence of which on the Cape York Peninsula seems a possibility, although it has yet to be proved) would probably hybridise to a significant extent in nature and that the latter should therefore be treated as a subspecies. Perry (1950) came to the opposite conclusion with regard to *Aëdes scutellaris* (called by him *Aëdes hebrideus* Edwards) and *Aëdes pernotatus* Farner & Bohart, which he crossed in the New Hebrides, where they are sympatric. The cross was partially successful in one direction. The hybrids resembled the female parent (*A. hebrideus*) in most respects, but some intergrading was observed. All the hybrid offspring were females and they were mated with *A. pernotatus* males. The infertility and mortality rates were high, but four viable male and non-viable female adult offspring were produced. Intergrading was more pronounced than in the F_1. In view of the small numbers of viable offspring Perry considered that no significant degree of successful hybridisation would take place in nature and that this was confirmed by his failure to observe any intergrading in wild populations of the two species. The only form other than *A. scutellaris katherinensis* to which subspecific status has so far been suggested is *A. pseudoscutellaris polynesiensis* Marks. In the course of her studies on variation in *A. pseudoscutellaris* (see above) Marks (1951) was led to apply a new name (*A. polynesiensis*) to "the generally recognised vector of filariasis" over a large part of Oceania, restricting the older name to a closely similar species apparently restricted to Fiji. Since this time Rozeboom and Gilford (1954*b*, and see Rozeboom, 1954) and Woodhill (1954) have crossed the two forms concerned. Crossing was successful in both directions, though with a marked reduction of hatching rate in the F_1 eggs, this reduction being greater when *A. polynesiensis* was used as the father than when it was used as the mother. Rozeboom and Gilford observed a definite preference for mates belonging to the same form and considered that although this was not sufficiently marked to prevent cross-mating in the laboratory the effect might be magnified in the natural environment. They preferred to postpone a decision as to whether the two forms should be treated as species or subspecies or relegated to a lower taxonomic category until field studies have shown whether there exists an effective barrier to mating in nature and as to whether or not they are microgeographically allopatric in Fiji. Woodhill drew similar conclusions and also stressed the desirability of testing the form of *A. polynesiensis* actually occurring in Fiji. (His own material came from Tahiti and the strain employed by Rozeboom and Gilford came from Samoa). It is evident that this group

affords admirable material for the study of speciation and it is greatly to be hoped that work on it will continue. That this work may also have results of medical interest is suggested by recent studies on the transmission of filariasis by species of the *A. scutellaris* group in Fiji (Manson-Bahr and Muggleton, 1952).

Summary.

An account is given of certain remarkable phenomena encountered while cross-breeding mosquitoes in the laboratory. The *Culex pipiens* and *Aëdes scutellaris* groups are the subject of much active research at the present time, but *Aëdes aegypti* and *Aëdes albopictus*, the crosses between which are in many ways the most remarkable, are currently neglected. Much current work on genetics, cytology, cytochemistry and serology bears directly on these crossing experiments and an attempt is made to show how they may be of interest to the general biologist and the epidemiologist as well as to the geneticist and the taxonomist.

References.

Altenburgg, E., 1945, *Genetics*. New York.

Barr, A. R., 1954, Hybridisation experiments with some American dark-winged Anophelines. *Exp. Parasit.* **3** : 445–457.

—— and Kartman, L., 1951, Biometrical notes on the hybridisation of *Culex pipiens* L. and *C. quinquefasciatus* Say. *J. Parasit.* **37** : 419–420.

Bergroth, E., 1889, Zwei neue Diptera. *Wien. ent. Ztg.* **8** : 295–298.

Bonnet, D. D., 1950, The hybridisation of *Aëdes aegypti* and *Aëdes albopictus* in Hawaii. *Proc. Hawaii. ent. Soc.* **14** : 35–39.

Callan, H. G. and Montalenti, G., 1947, Chiasma interference in mosquitoes. *J. Genet.* **48** : 119–134.

Callot, J., 1947, Étude sur quelques souches de *Culex pipiens* (sensu lato) et sur leurs hybrides. *Ann. Parasit. hum. comp.* **22** : 380–393.

——, 1954, Le rapport trompe/palpes dans les biotypes du complexe *Culex pipiens* et leurs hybrides. *Ibid.* **29** : 131–134.

Carpenter, S. J., Middlekauff, W. W., and Chamberlain, R. W., 1946, The mosquitoes of the southern United States east of Oklahoma and Texas. *Amer. Midl. Nat., Monogr.* No. 3.

Christophers, S. R., 1947, Mosquito repellents, being a report of the mosquito repellent inquiry, Cambridge 1943–5. *J. Hyg., Camb.* **45** : 176–231.

Cleland, R. E., 1936, Some aspects of the cyto-genetics of *Oenothera*. *Bot. Rev.* **2** : 316–348.

Clements, A. N., 1954, *The metabolism of mosquitoes with particular reference to ovary development and flight*. Ph.D. Thesis, Cambridge.

De Buck, A., 1942, Kreuzungsversuche mit *Stegomyia fasciatus* Fabricius and *S. albopicta* Skuse. *Z. angew. Ent.* **29** : 309–312.

Dobrotworsky, N. V., 1955, The *Culex pipiens* group in south-eastern Australia. IV. Crossbreeding experiments within the *Culex pipiens* group. *Proc. Linn. Soc. N.S.W.* **80** : 33–43.

—— and Drummond, F. H., 1953, The *Culex pipiens* group in south-eastern Australia : II. *Ibid.* **78** : 131–145.

Downs, W. G., and Baker, R. H., 1949, Experiments in crossing *Aëdes* (*Stegomyia*) *aegypti* Linnaeus and *Aëdes* (*Stegomyia*) *albopictus* Skuse. *Science* **109** : 200–201.

Farid, M. A., 1949, Relationships between certain populations of *Culex pipiens* Linnaeus and *Culex quinquefasciatus* Say in the United States. *Amer. J. Hyg.* **49** : 83–100.

Frizzi, G., 1947, Salivary gland chromosomes of *Anopheles*. *Nature, Lond.* **160** : 226–227.

Ghelelovitch, S., 1950, Étude génétique de deux caractères de pigmentation chez *Culex autogenicus* Roubaud. *Bull Biol.* **84** : 217–224.

——, 1952, Sur le déterminisme génétique de la stérilité dans les croisements entre différentes souches de *Culex autogenicus* Roubaud. *C.R. Acad. Sci., Paris,* **234** : 2386–2388.

Gilchrist, B. M., and Haldane, J. B. S., 1947, Sex linkage and sex determination in a mosquito, *Culex molestus*. *Heriditas, Lund.* **33** : 175–190.

Golberg, L. and De Meillon, B., 1948, The nutrition of the larva of *Aëdes aegypti* Linnaeus. 3. Lipid requirements. 4. Protein and amino-acid requirements. *Biochem. J.* **43** : 372–387.

L'Héritier, P., 1951, The CO_2 sensitivity problem in *Drosophila*. *Cold Spr. Harb. Symp. quant. Biol.* **16** : 99–112.

Hinman, E. H., 1937, A study of the food of mosquito larvae (Culicidae). *Amer. J. Hyg.* **12** : 238–270.

Hoang Tich Try, 1939, Essai de croisement de *St. albopicta* ♀ et *St. fasciata* ♂ en espace restreint. *Bull. Soc. Path. exot.* **32** : 511–513.

Hosoi, T., 1954, Egg production in *Culex pipiens pallens* Coquillett. I : Seasonal changes. II : Influence of light and temperature on activity of females. III : Growth and degeneration of ovarian follicles. IV : Influence of breeding conditions on wing length, body weight and follicle production. V : Relation to fattening and biting activity. *Jap. J. med. Sci. Biol.* **7** : 57–73, 75–81, 111–127, 129–134, 231–240.

Howard, L. O., Dyar, H. G., and Knab, F., 1915, *The mosquitoes of North and Central America and the West Indies :* III. Washington.

Huttel, V., 1950, Note sur la répartition des moustiques dans le Bas-Dahomey. *Bull. Soc. Path. exot.* **43** : 563–566.

Joyet-Lavergne, P., 1941, Étude comparée de l'influence de divers sucres, glucose, lévulose, galactose, dans l'action de la vitamine B_2. *C.R. Acad. Sci., Paris,* **212** : 726–729.

Kartman, L., 1953, Factors influencing infection of the mosquito with *Dirofilaria immitis* (Leidy, 1856). *Exp. Parasitol.* **2** : 27–78.

Kitzmiller, J. B., 1953*a*, Mosquito genetics and cytogenetics. *Rev. bras. Malariol.* **5** : 285–359.

——, 1953*b*, Étude de souches de laboratoire de *Culex pipiens* et *Culex fatigans*. *Ann. Parasit. hum. comp.* **28** : 321–325.

—— and Clark, C. C., 1952, Salivary gland chromosomes in mosquitoes. *Genetics* **37** : 596.

Knight, K. L., 1953, Hybridisation experiments with *Culex pipiens* and *C. quinquefasciatus* (Diptera : Culicidae). *Mosquito News* **13** : 110–115.

—— and Abdel Malek, A. A., 1951, A morphological and biological study of *Culex pipiens* in the Cairo area of Egypt. *Bull. Soc. Fouad Ier Ent.* **35** : 175–185.

Laven, H., 1951, Crossing experiments with *Culex* strains. *Evolution* **5** : 370–375.

——, 1953, Reziprok unterschiedliche Kreuzbarkheit von Stechmücken (Culicidae) und ihr Deutung als plasmatische Vererbung. *Z. indukt. Abstamm.-u. VererbLehre* **85** : 118–136.

——, and Kitzmiller, J. B., 1954, Kreuzungsversuche zwischen europäischen und amerikanischen Formen des *Culex-pipiens*-Komplexes. *Z. Tropenmed. u. Parasit.* **5** : 317–323.

LAVEN, H., 1955, Erbliche intersexuali tät bei *Culex pipiens*. *Naturwissenschaften* **42** : 517.

——, 1956*a*, Cytoplasmic inheritance in *Culex*. *Nature, Lond.* **177** : 141–142.

——, 1956*b*, X-ray induced mutations in mosquitoes. *Proc. R. ent. Soc. Lond.* (A) **31** : 17–19.

LAWLOR, W. K., 1949, *Immunological studies of antigen extracted from mosquitoes and their application in taxonomy*. M.Sc. Thesis, University of California.

LINNAEUS, C., 1762, *D. F. Hasselquists. . . . Reise nach Palestina*. Rostock.

MACGILCHRIST, A. C., 1913, *Stegomyia* Survey, Port of Calcutta, *Proc. 3rd Meeting General Malaria Committee* Madras, pp. 193–196.

MANSON-BAHR, P. and MUGGLETON, W. J., 1952, Further research on Filariasis in Fiji. *Trans. R. Soc. trop. Med. Hyg.* **46** : 301-326.

MARKS, E. N., 1951, The vector of Filariasis in Polynesia : a change in nomenclature. *Ann. trop. Med. Parasit.* **45** : 137–140.

——, 1954, A review of the *Aëdes scutellaris* subgroup with a study of variation in *Aëdes pseudoscutellaris* (Theobald) (Diptera, Culicidae). *Bull. Brit. Mus.* (*Nat. Hist.*) (Ent.) **3** : 349–414.

MARSHALL, J. F., 1938, *The British mosquitoes*. London.

—— and STALEY, J., 1937, Some notes regarding the morphological and biological differentiation of *Culex pipiens* Linnaeus and *Culex molestus* Forskål (Diptera : Culicidae). *Proc. R. ent. Soc. Lond.* (A) **12** : 17–26.

MATTINGLY, P. F., 1953, The subgenus *Stegomyia* (Diptera, Culicidae) in the Ethiopian Region. II : Distribution of species confined to the East and South African Sub-region. *Bull. Brit. Mus.* (*Nat. Hist.*) (Ent.) **3** : 1–65.

——, 1954, Notes on the subgenus *Stegomyia* (Diptera, Culicidae), with a description of a new species. *Ann. trop. Med. Parasit.* **48** : 259–270.

—— and CHWATT, L. J., 1954, Morphology and bionomics of *Aëdes* (*Stegomyia*) *pseudoafricanus* Chwatt (Diptera, Culicidae) with some notes on the distribution of the subgenus *Stegomyia* in Africa. *Ibid.* 183–193.

——, KNIGHT, K. L., LAVEN, H. and SHUTE, P. G., 1953, The *Culex pipiens* complex. *Trans. Int. Congr. Ent. IX.* **2** : 283–300.

——, ROZEBOOM, L. E., KNIGHT, K. L., LAVEN, H., DRUMMOND, F. H., CHRISTOPHERS, S. R. and SHUTE, P. G., 1951, The *Culex pipiens* complex. *Trans. R. ent. Soc. Lond.* **102** : 331–382.

MICKS, D. W., 1954, Paper chromatography as a tool for mosquito taxonomy : the *Culex pipiens* complex. *Nature, Lond.* **174** : 217–218.

PERRY, W. J., 1950, Biological and crossbreeding studies on *Aëdes hebrideus* and *Aëdes pernotatus*. *Ann. ent. Soc. Amer.* **43** : 123–136.

QUTUBUDDIN, M., 1952, The emergence and sex ratio of *Culex fatigans* Wied. (Diptera, Culicidae) in laboratory experiments. *Bull. ent. Res.* **43** : 549–565.

ROZEBOOM, L. E., 1953, Sexual isolation in some North American *Anopheles* mosquitoes. *Amer. J. trop. Med. Hyg.* **2** : 677–682.

——, 1954, Hybridisation among mosquitoes and its possible relation to the problem of insecticide resistance. *J. econ. Ent.* **47** : 383–387.

—— and GILFORD, B. N., 1954*a*, Sexual isolation between populations of the *Culex pipiens* complex in North America. *J. Parasit.* **40** : 237–244.

——, 1954*b*, The genetic relationships of *Aëdes pseudoscutellaris* Theobald and *A. polynesiensis* Marks (Diptera : Culicidae). *Amer. J. Hyg.* **60** : 117–134.

SCHUH, J. E., 1951, Some effects of colchicine on the metamorphosis of *Culex pipiens* Linn. *Chromosoma* **4** : 456–469.

SIMONETTI, A., 1952, Studio sulla possibilità d'incrocio fra *Culex pipiens* L. e *Culex autogenicus* R. *Riv. Biol.* **44** : 117–133.

SIMMONS, J. S., ST.JOHN, J., and REYNOLDS, F. H. K., 1930, Transmission of Dengue Fever by *Aëdes albopictus* Skuse. *Philipp. J. Sci.* **41** : 215–229.

Smith-White, S., 1950, A note on non-reciprocal fertility in matings between subspecies of mosquitoes. *Proc. Linn. Soc. N.S.W.* **75** : 279–281.

Summers-Connal, S. L. M., 1926, On the numerous variations occurring in the specimens of *Aëdes argenteus* Poiret obtained in Lagos, Nigeria. *Annu. med. sanit. Rep. Nigeria*, pp. 132–139.

——, 1927, On the variations occurring in *Aëdes argenteus* in Lagos, Nigeria. *Bull. ent. Res.* **18** : 5–11.

Sutton, E., 1942, Salivary gland type chromosomes in mosquitoes. *Proc. nat. Acad. Sci., Wash.* **28** : 268–272.

Teesdale, C., 1955, *Studies on the bionomics of* Aëdes aegypti (L.) *in its natural habitats in a coastal region of Kenya. Bull. ent. Res.* **46** : 711–742.

Toumanoff, C., 1937, Essais préliminaires d'intercroisement de *St. albopicta* Skuse avec *St. argentea* Poiret *s. fasciata* Theob. *Bull. Soc. med.-chir. Indoch.* **15** : 964–970.

——, 1938, Nouveaux faits au sujet de l'intercroisement de *St. albopicta* Skuse avec *St. argentea s. fasciata* Theob. *Rev. med. franc. Extr. Or.* **17** : 365–368.

——, 1939, Les races géographiques de *St. fasciata* et *St. albopicta* et leur intercroisement. *Bull. Soc. Path. exot.* **32** : 505–509.

——, 1950, L'intercroisement de l'*Aëdes* (*Stegomyia*) *aegypti* L. et *Aëdes* (*Stegomyia*) *albopictus* Skuse. Observations sur la mortalité dans descendance des générations hybrides F_1 et F_2 de ces insectes. *Ibid* **43** : 234–240.

Trager, W., 1937, A growth factor required by mosquito larvae. *J. exp. Biol.* **14** : 240–251.

Waddington, C. H., 1954, The cell physiology of early development. *Proc. 7th Symp. Colston Res. Soc.*, pp. 105–119.

Waterhouse, D. F. and Paramonov, S. J., 1950, The status of the two species of *Lucilia* (Diptera, Calliphoridae) attacking sheep in Australia. *Aust. J. Sci. Res.* (B) **3** : 310–336.

Weyer, F., 1936, Kreuzungsversuche bei Stechmücken. *Arb. physiol. angew. Ent., Berl.*, **3** : 202–208.

Woodhill, A. R., 1949, A note on experimental crossing of *Aëdes* (*Stegomyia*) *scutellaris scutellaris* Walker and *Aëdes* (*Stegomyia*) *scutellaris katherinensis* Woodhill (Diptera : Culicidae). *Proc. Linn. Soc. N.S.W.* **74** : 224–226.

——, 1950, Further notes on experimental crossing within the *Aëdes scutellaris* group of species (Diptera : Culicidae). *Ibid.* **75** : 251–253.

——, 1954, Experimental crossing of *Aëdes* (*Stegomyia*) *pseudoscutellaris* Theobald and *Aëdes* (*Stegomyia*) *polynesiensis* Marks (Diptera : Culicidae). *Ibid.* **79** : 19–20.